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ABOUT THE PROCESS OF ABSCISSION OF SOFT PLANT ORGANS

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## ABOUT THE PROCESS OF ABSCISSION OF SOFT PLANT ORGANS

(Following is the translation of an article by Hugo V. Mohl, Tübingen, *Botanische Zeitung*, (Botanical News), No. 31, August 3, 1860, pages 273-277. Translation performed by Constance L. Lust.)

In my earlier treatise about leaf abscission (*Botan. Zeit.* 1860, No. 1) I stated that I investigated only a very specific case of abscission of leaves of all the wide-spread cases available in the plant world. Only more extensive investigations would show if in the abscission of other organs (eg. twig tips, blossoms, and others) the same organic processes were responsible as for abscission of leaves. It may be of distinct value to return to these organic processes and report our findings.

In the previous paper I showed that the abscission of leaves is not based on a peculiar structure of the leaf joint. This, to be sure, is already present before abscission. The synthesis of the separation layer is dependent on a change of structure of the usual parenchyma cells, and that this process only begins shortly before the leaf falls off. It is independent of a periderma of the joint, but does need another process. The synthesis of the abscission cells and the separation of leaves caused by them can appear earlier if an external, injurious influence acts upon the leaf. For this reason many woody-plants south of the Alps retain their leaves several months longer in the year than those to the north.

It is well known that under certain situations leaves can defoliate early. This upsets the plant collector often, because at times these situations prevent him from collecting and drying his plants fast enough. The leaves are dropping off very rapidly. This condition caused me to utilize young leaves - not even fully developed, in order to ascertain if the same organic processes were occurring when young leaves drop off as in autumn when the others are dropping naturally. I took cut-off branches of several trees in June and put them in water in order to avoid the drying out of the leaves. I already knew from previous studies in what way they defoliated in autumn. The results were surprising in some cases. The leaves of *Gymnocladus canadensis*, which were not yet fully grown, were tightly attached to the stem and the cell tissues of the leaves merged with the stem of the leaf without any visible demarcation zone. After 48 hours in the water the situation looked completely different. The leaves dropped off under the slightest shaking and a very smooth abscission surface remained. Microscopic examination showed in these leaves that as in those that dropped in autumn an amylum (starch)-containing layer was formed between leaf and the stem. After abscission the cells formed into a round structure which was called the abscission layer.

The same phenomenon was observed in the leaves of *Ailantus glandulosa*, only the abscission layer formed much later; it started to develop at day three and was fully formed by day four.

In order to form a separation-layer in the joint of the area common to the stems, a somewhat longer time was required in the capsule for both plants. This was fully developed by day six to seven. Then, the abscission of the stem of the leaf from the twig followed after only a slight touching. The scar on the leaf as well as on the stem both looked very smooth, much as do the crown-petals of many flowers. This is because the abscission surfaces are formed from epidermis as are the cells of the crown petals of flowers, and they reflect light in the same manner. The separation of these immature leaves is effected, after the abscission layer is formed, almost easier than do the leaves that drop in autumn. The stronger, woody fiber bundles of the mature growth separate with more difficulty. The anatomical study of the joints of these youthful leaves showed that during the formation of the abscission layer not only the parenchyma cells of the joint were involved, but also that the immature cells of the fibers separated from each other and extended their rounded-off ends toward the abscission surface. The only difference between the fast developing abscission layer caused by external conditions and that which develops slowly in the autumn, existed in the fact that the cells contained no amyllum in most cases. This also is the case in some separation layers of plants which develop naturally in autumn. An extraneous fact should be mentioned; that no trace of a periderm could be found in the leaves of *Gymnocladus* when the stem joint separated in the fall. Also, the brown pigmentation was absent in the parenchyma of the separation layer. This is quite noticeable in the fall in certain plants. It is lacking in other varieties. All cells of the joint of the leaf were completely moist (juicy) and fresh.

The leaves of *Fraxinus excelsior* behaved in an analogous manner. On the fourth day a separation layer began to be formed at the base of the leaves and they were completely formed at day five. On this day also the formation of pair of nodes at the insertion point where the separation layer crossed the stem of the leaf. The development occurred at the base of the main stem of the leaf. A few days more were required for the complete formation of the latter. With *Juglans regia* the small leaf-stems of the small leaves contained the abscission layer completely formed by day five.

Under similar conditions the abscission layer also develops with equal speed in the joint of simple leaves. At this time of year (June) one can see no evidence for this in the fresh leaf. The same situation was seen with *Amygdalus communis* and *Asimina triloba*. On day three and four the layer was completely formed. In *Catalpa bignonioides* it was formed by day six. Let us look at another proposal, which I always found attractive but was usually avoided by most writers active in research on vegetation of trees. This involves, that many wood-plants already drop their little leaves leaving a scar. This occurs during late summer, but sometimes as early as June. There is an analogy in general plant physiology concerning longitudinal growth of woody plants which develop a bud in the joint area. It should be noted that similar occurrences appear in trees during the so-called second growth. Under

good conditions these trees throw off their twig tips which had become a terminal bud, but in the same year this will grow into a branch. I saw this in a very young linden tree, growing in good soil. The total growth of the year was enhanced over what would normally be expected. This same "double year's growth" I also noted in an oak tree which had been planted in good soil. As far as I know, no other author has investigated this releasing mechanism more extensively. Therefore I thought it worth while to investigate this process. Especially I wanted to ascertain whether the principles were the same as for abscission of leaves. This assumption proved to be fully correct.

For these observations *Gymnocladus*, *Catalpa bignonioides* as well as varieties of *Gleditschia* and *Tilia* served as excellent materials, but above all *Ailantus glandulosa*. In all instances the releasing of the twig tip depended on the separation of the amyllum containing or protein-rich cells of the dividing layer which corresponded in each case with the respective leafjoints. Particularly with *Ailantus* it was very clear that the formation of the dividing layer involved the parenchyma cells as well as those cells of the vascular tissue that had not yet gone to wood. No trace of periderma was evident here as had developed under the epidermis of the twigs in June.

It seemed to be important to look at those leaves that had been transformed into branches of *Phyllocladus* and *Xylophylla* and others. At the time I wanted to study this only *Xylophylla latifolia* was in the state of development that I wanted in which I could study the abscission of the branches. Therefore my observations are limited to this plant. On this one can find two kinds of "abscission branches", first those that represent the stem of the pinnate leaves; secondly those that are found in a double row, spread out fan-like, the leaflets resembling little boughs. The first-mentioned branches are so similar to the common stem that even the furrow running along the upper side of many leaves is present, the swollen end passing through a ring-like furrow, marking the joint, sets it apart from the trunk. This joint, as well as that at the base of the single leaflet, is saturated internally with a thin layer of small parenchyma cells which contain many crystal glands (openings) and starch granules. The middle part of this small-celled layer develops in the ordinary way into a dividing layer by which the above-mentioned boughs get separated and leave a smooth scar behind. Even here, as with pinnate leaves, one can form the dividing layer by keeping cut twigs in a tin-can. With *Phyllocladus* no results were obtained with this method.

My attention was further turned to the abscission of blossoms. The pistil of *Aesculus* and *Pavia* were especially useful in this regard. It is known that blossoms of these trees turn into chymes, and the blossom stems of the male part are released and leave a smooth scar. The center part and later a large part of the fruits also fall off. All these abscissions depend equally on the synthesis of a dividing layer, whose cells release after they become large and round off. Here also no periderm was evident.

The male blossoms of Cucurbitaceae (Cucumis, Melo, Lagenaria vulgaris) also release by means of a separation layer, similar to Aesculus. The layer is formed at the edge between the blossom stem on the blossom itself.

Hermaphrodite blossoms also fall off whole, if they do not bear fruits. The blossom of *Hemerocallis flava* and *fulva* are examples of this. In this area these plants do not bear fruits. The blossom remains on the stem for a few days while the large part of the perigonium wilts. However, the lower part of the perigonium and the ovary remain juicy. A separation layer is formed at the base of the blossom above the stem; the cells round off and separate without formation of starch. This results in the release of the blossom.

It could be assumed that the individual blossom-organs behaved as leaf-structures during their own abscission. Since the investigations, which I started about this, substantiated this fact, I didn't think it necessary to study a large number of blossoms. It may be that some special details are different in different species.

The abscission of perigon-leaves was investigated in *Lilium bulbiferum* and *L. Martagon*. The perigon leaves of these plants wilt, whereby the lower portion of them still remain rather wet. Abscission follows after separation and rounding off of the cells of the dividing layer. This contained no starch granules.

A definite dividing zone was similarly found at the time of abscission in *Papaver somniferum*, *Liriodendron Tulipifera*, *Mirabilis Jalapa*, *Datura Stramonium*, *Rosa canina*, *Glaucium luteum*, *Lonicera Caprifolium*, *Rhododendron ponticum*, *Lilium bulbiferum*, *L. Martagon*, *Dictamnus Fraxinella*.

In most cases the cells of the dividing layer did not contain any more starch than the cells in neighboring tissues. Only the cells of the dividing layer of the petals of *Liriodendron* were an exception. They had a high content of amyllum (starch) as did the cells of the abscission layer of the leaves which fell off in fall. It may be that when the plant blooms for a long time that the layer develops more slowly than in rapid flowering plants. In the latter the abscission layer often develops in a few hours; eg. during the night; in some cases during the afternoon hours.

If the crown of the blossom falls off relatively fresh, (as is usually the case) then the cells of the dividing layer are very juicy. They are colored brown due to the liquid inside them and not because of decomposition. Gartner (Beitr. z. Kenntn. d. Befruchtung d. Gew. I. 52) offered the opposite view. He maintained that the edge is colored brown because of the decomposition of dead cells. After the abscission, when the parenchyma cells are exposed to air, the cells may become brown as is seen in a cut edge of healthy plant organs. This has, however not been observed during abscission. This aspect was not studied under the microscope; the bare eye, or the magnifying glass are wholly inadequate.

It can be seen from the previous discussion that the same internal process repeats itself regardless of whether it be stem or leaf that is being separated. The primary aspect of this abscission process is that separation is brought about by the formation of a dividing layer. Eventually the rounded cells force a breaking of a part of vascular fibers. An increase in cells in the area surrounding the layer did not occur. In the organs of blossoms this seemed to happen in the leaves falling off in autumn. An increase in protein content was observed in the cells, as well as loosening, rounding off of cells and enlargement of cells. The soft, vascular cells gave the dividing surface a velvet appearance, or they appear starchy as when the cell layer of the male blossom of *Lagenaria* separated.

It is obvious that one should not confuse the abscission of succulent organs with a drying up (and in this way release the organ) of an organ whereby the cells are torn apart during drying. The latter is a wholly mechanical result of the hygroscopic conditions of the dried tissue. Abscission depends on organic action of the living plant. It is not reasonable to consider that this process has a type of articulation of hollow organs of the plant. The separation of the two processes is rather completely different. The important concept involved in abscission is that a dividing layer is formed. This layer can develop in the middle of a continuous organ similarly as a dividing line between organs. The formation of an articulation is simply a physiological process, and a morphological conclusion cannot be extracted. By similar reasoning it is also not permitted to conclude that the structure of ovaries of *Hyoscyamus* and *Nicotiana* are different because they exert their physiological function differently.